STUDIES IN THE FERN-GENERA ALLIED TO *TECTARIA* CAV. VI

A conspectus of genera in the Old World regarded as related to *Tectaria*, with descriptions of two genera

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Abstract

A brief conspectus of the palaeotropic genera, regarded by the author as related to *Tectaria* Cav., is presented with: comments on individual genera, descriptions of two new ones, *Chlamydogramme* and *Megalastrum*, some thoughts on inter-relationships, a key to the genera, and also brief comments on neotropic genera.

Introduction

In the first paper of this series (Holttum 1984, p. 314) is the following statement which was intended to show the differences between two groups of genera which together constitute almost the whole of the family Aspidiaceae as arranged by Pichi Sermolli (1977):

Dryopteris group. Midribs of ultimate leaflets grooved, the groove of the rachis bearing the leaflets being open to admit the leaflet-groove, the margin of the leaflet being decurrent (but not prominent) down the side of the rachis; ctenitoid hairs lacking.

Tectaria group. Midribs of ultimate leaflets more or less prominent (in *Tectaria* sometimes slightly grooved) and bearing ctenitoid hairs, usually many.

While working on a monograph of the genus *Ctenitis* in Asia, Malesia and the Western Pacific I discovered the existence within *Ctenitis* as arranged by Ching (1938) of a group of species (his suggested subgenus *Dryopsis*) which has pinna- or pinnule-midribs grooved but with the groove closed near the junction of the pinna with the rachis which bears it. In these species the hairless groove has on its borders thick-based hairs (the cells near the base wider than long) like those in a similar position in *Peranema* and *Nothoperanema*, also some structures which are narrowly scale-like above a similar thick base; these are quite unlike anything in true *Ctenitis* and the species differ from typical *Ctenitis* also in other ways. Mr P.J. Edwards assisted me to make a detailed comparative study of all such species, which we have assigned to a new genus *Dryopsis* in paper II of the present series. The detailed studies show that the distal part of some of the peculiar hairs resembles a single hair of *Ctenitis*. Thus *Dryopsis* may be a connecting link between the *Tectaria* and *Dryopteris* groups of genera. Furthermore, in some genera of the *Tectaria* group the multicellular hairs on the raised upper surfaces of costae are more or less acicular, not contorted on drying as in *Ctenitis*. My distinction between the two groups of genera will therefore need to be modified. I still believe however that the genera I associated together in 1947 as a subfamily Tectarioideae are a natural group.

I have now examined the types of almost all species in the Old World (including Africa) assigned to genera of the *Tectaria* group and here summarize significant information about them in the form of a tentative conspectus, with descriptions of two new genera and some thoughts on their possible inter-relationships, followed by an artificial key. I intend to prepare an account of Malesian species based on this scheme for *Flora Malesiana,* where I hope to publish the facts about them in more detail, and to make formal transfer of some names.

The genera closely associated with *Tectaria* have (where known) 40 chromosomes and lack cylindric glands. The remaining genera have (where known) 41 chromosomes and are divided into two groups, those with and without glands. The genera are arranged below in these categories; possible inter-relationships between members of the categories are then considered.

Tectaria and closely allied genera

Common characters: scales narrow, consisting wholly of narrow cells, never clathrate, rarely abundant on smaller axes of the frond; ctenitoid hairs always present on the upper surface of the rachis; venation and branching (apart from basal pinnae) almost always catadromous; veins all free or variously anastomosing; unicellular cylindric glands lacking; sori in most species indusiate but in some exindusiate and ± spreading along veins, in a few, where the fertile lamina is much contracted, spreading along all veins and covering the whole of the lower surface; chromosome number, where known, 40.

Tectaria Cav.

Anales Hist. Nat. 1: 115 (1799)

This is much the largest genus, consisting of about 210 species of which 40 are neotropic. The best subdivision (not quite a sharp one) appears to be between species (including the type) which have amply anastomosing veins with free branched veinlets in the areoles, and those which have either free veins or veins forming narrow costal areoles lacking included free veinlets and few included veinlets in other areoles (venation of *Sagenia* Presl). A separation of species which are wholly free-veined is not possible; in *T. fuscipes* (Bedd.) C. Chr. sterile fronds have veins forming costal areoles but fertile ones have all veins free. I thus propose to treat *Tectaria* as consisting of two sections.

Sect. **Tectaria**

Including *Hemigramma* (M.G. Price 1974) and *Quercifilix* (W.A. Sledge 1972).

The type species of *Hemigramma*, *H. latifolia* (Goldm.) Copel. (= *Tectaria hilocarpa* (Fée) Price), has simple fronds, the fertile ones much constricted with a simplified venation and sporangia borne all along the closely crowded veins (pl. 1). Copeland (1908) showed that hybrids were formed in Luzon between this and *Tectaria crenata* Cav. In 1928 he enlarged *Hemigramma* by including in it *Gymnopteris decurrens* Hook. from Hong Kong and allied species. But the latter have broader fertile pinnae than the simple fertile fronds of *H. latifolia,* with an ample venation exactly as in the sterile pinnae, and a species in the Malay Peninsula has sori intermediate in form between those of *H. decurrens* and and species of *Tectaria* which have many small sori. Thus *H. latifolia* and *H. decurrens* are related to different species of *Tectaria*. In both, the sporangia are borne all along the veins on a restricted surface. The same is true of the only species of *Quercifilix*, which hybridizes with *Tectaria decurrens* in Ceylon. The species originally named *Leptochilus pentagonalis* R. Bonap., transferred with doubt to *Hemigramma* by Christ-

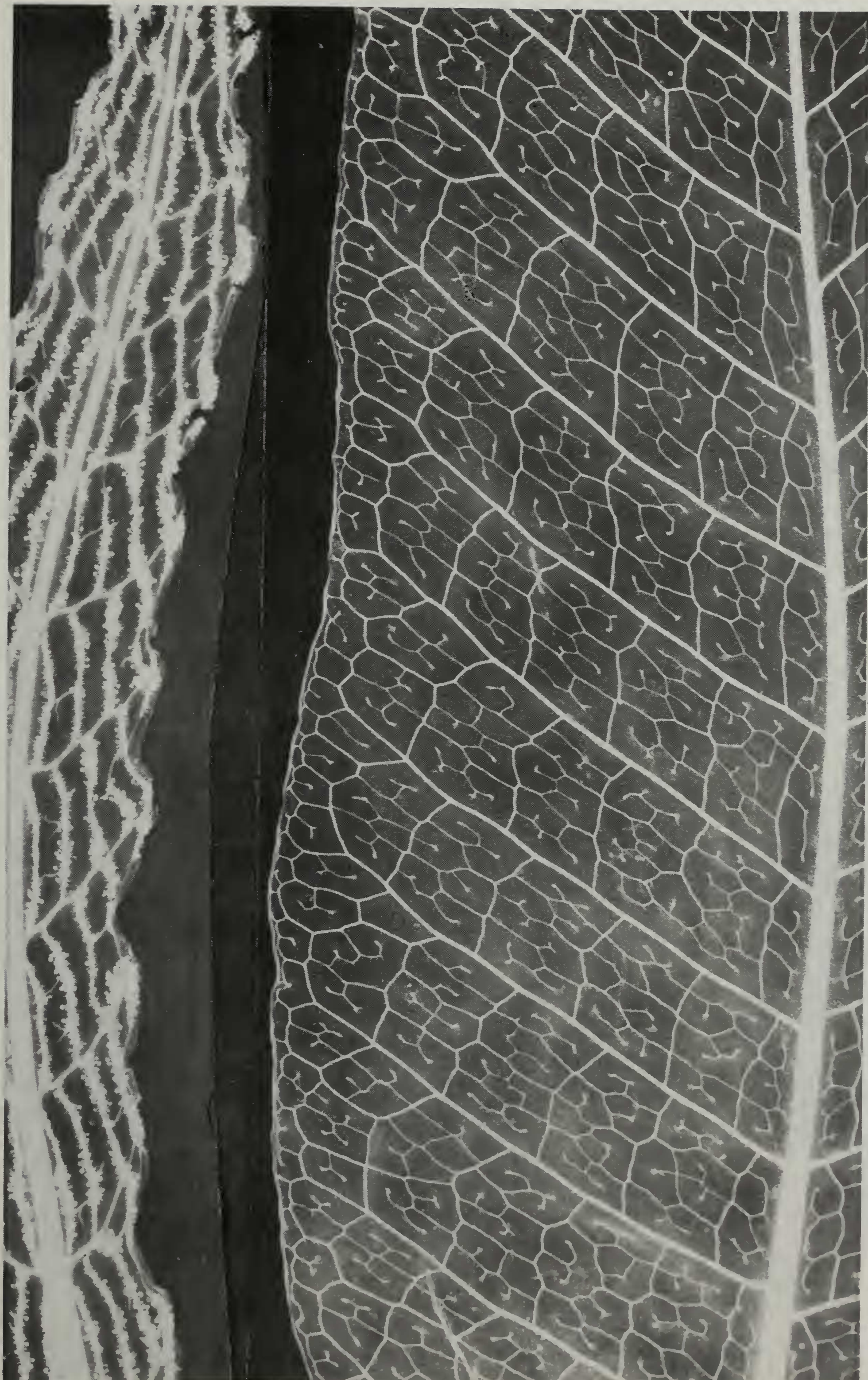


Plate 1. *Hemigramma latifolia* (Goldm.) Copel. = *Tectaria hilocarpa* (Fée) Price: venation of fertile (× 4.5) and sterile (× 3) fronds; Java, *Schiffner* s.n. (L).

A

C

D

B

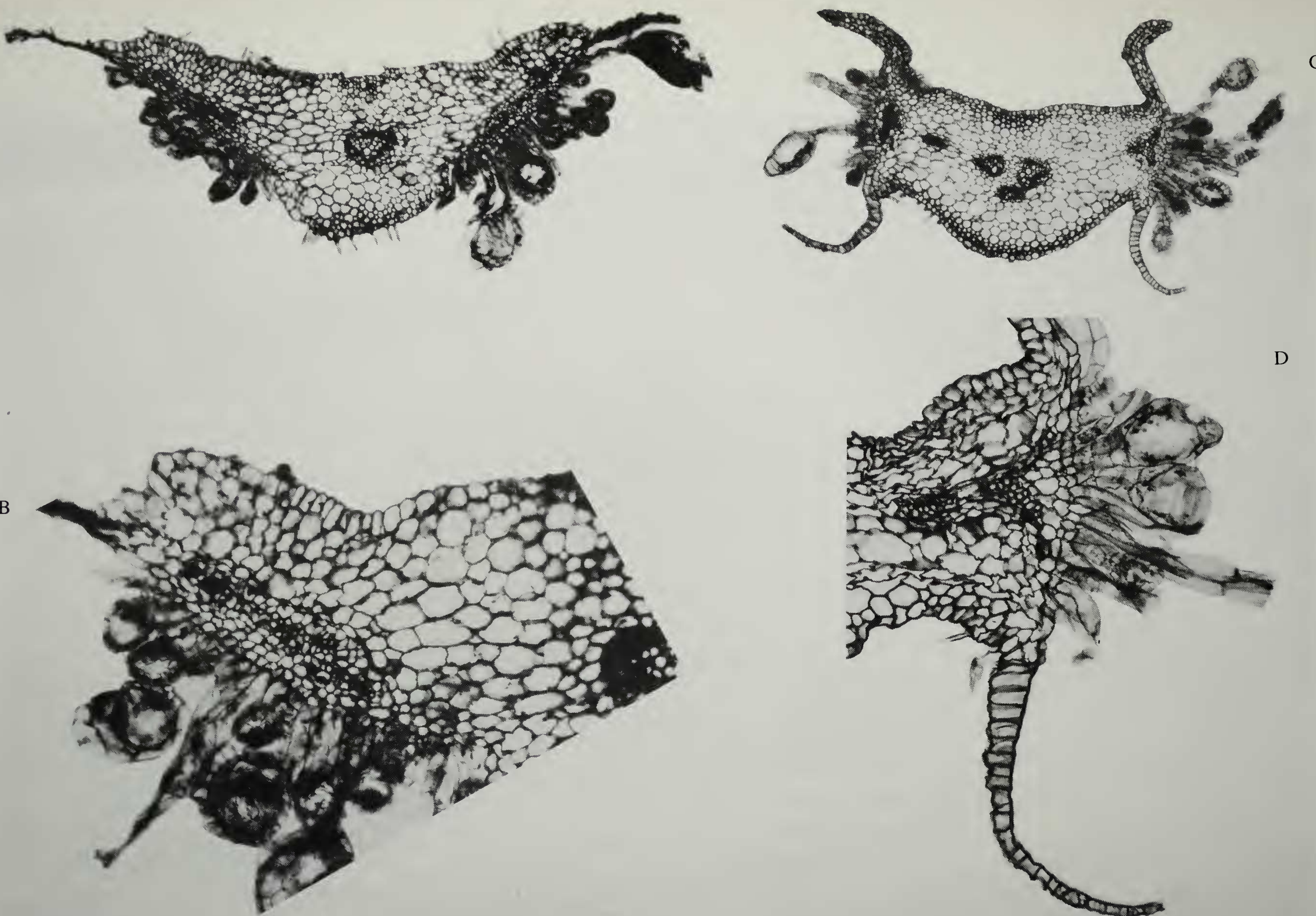


Plate 2. Transverse sections of fertile pinnae. *Hemigramma siifolia: A* (× 2.7), *B* (× 6.7); *Elbert 673*, Lombok (L). *Chlamydogramme hollrungii: C* (× 2.7), *D* (× 6.7.); *Hoogland & Craven 10187*, Papua New Guinea, Sepik District (K).

ensen, appears to be nearer to *Quercifilix* than to any species of *Hemigramma* as arranged by Copeland.

Sect. **Sagenia** (Presl) Holttum, *stat. nov.*

Sagenia Presl, Tent. Pterid. 86 (1836), as regards venation. Type species (selected here): *Sagenia latifolia* Presl, l.c. fig. 23 = *Tectaria mexicana* (Fée) Morton, Amer. Fern Journ. 56: 133 (1966), not *T. latifolia* (Forst.) Copel.

Stenosemia Presl, which has sterile fronds with *Sagenia* venation and much-contracted fertile ones, also *Cionidium* Moore which has extra-marginal sori terminal on veins, are included here.

Species of sect. *Sagenia* which have all veins free are a minority. They are most abundant in mainland S.E. Asia; apart from the Philippines, very few occur in Malesia and the Pacific. I regard these free-veined species as representing the original form of the genus and S.E. Asia as its probable centre of origin. The largest fronds are borne by *T. ingens* (Atk.) Holttum of Sikkim, attaining a length of 3 m. Two free-veined species in the neotropics have been included in *Tectaria*: *T. brauniana* (Karst.) C. Chr. and *T. pedata* (Desv.) R. & A. Tryon. They are certainly not related to the free-veined species of Asia; see below for further comment.

Genera related to *Tectaria* sect. *Tectaria*

Tectaridium Copel.

Philip. J. Sci. 30: 329 (1926).

Sterile fronds simple and unlobed, with venation as *Tectaria* sect. *Tectaria*; fertile fronds lobed to the costa, the very narrow lobes bearing indusiate sori; intermediate forms are frequent. There is only one species, which does not appear to be nearly related to any species of *Tectaria*.

Chlamydogramme Holttum, *gen. nov.*

Generi Tectariae Cav. affinis; frondes pinnatae, valde dimorphae; pinnae frondis sterilis simplices, integrae, venis ut in *Tectaria* sect. *Tectaria* ordinatis; pinnae frondis fertilis anguste lineares, soris linearibus marginalibus laminae et indusiis prope costas in juventute tectis. Type species: *Chlamydogramme hollrungi* (Kuhn) Holttum, **comb. nov.**

(*Gymnopteris hollrungii* Kuha in Schum. & Hollrung. Fl. Kaiser Wilhelmsl.: 8 (1889); *Hemigramma hollrungii* (Kuhn) Copel.)

Chlamydogramme hollrungi (Kuhn) Holttum *comb. nov.*

This species has fronds very similar in general aspect to those of the species from Lombok originally described as *Leptochilus siifolius* by Rosenstock and also transferred to *Hemigramma* by Copeland, but with a continuous indusium (not noticed by Copeland) along each side of the pinna-midrib in fertile pinnae; sections of fertile pinnae of the two species are shown in plate 2.

Chlamydogramme is comparable to the tropical American genus *Dictyoxiphium* Hook. but the latter has simple fronds, the fertile ones not greatly constricted so that the continuous indusium is not near the midrib. The two genera are not nearly related.

Genera related to *Tectaria* sect. *Sagenia*

Heterogonium Presl, emend. Holttum

Kalikasan 4: 205-231 (1975).

Basal pinnae always narrowed towards their bases on the basiscopic side; vena-

tion as in *Tectaria* sect. *Sagenia* even in fronds with broad pinnae, only differing in less frequent free veinlets in non-costal areoles; sori often exindusiate and variously ± elongate along the veins, in a few species running along all veins in a constricted fertile lamina; about 20 species, mainly Malesian.

Though the shape of the basal pinnae is the only constant character distinguishing species of this genus from those of *Tectaria* sect. *Sagenia*, they collectively have a variety of other characters and appear to form a natural group which is more sharply distinct from *Tectaria* sect. *Tectaria* than is sect. *Sagenia*. The only evidence I have seen of hybridization with species of *Tectaria* sect. *Sagenia* is provided by some Philippine specimens, collected by M. G. Price, which appear to be hybrids between *H. pinnatum* (Copel.) Holttum (a tetraploid with constricted fertile fronds) and *Tectaria aurita* (Sw.) S. Chandra (Stenosemia aurita Presl), which T.G. Walker (1973) found also to be a tetraploid with n = 80.

R.C. Ching (1938) has proposed a genus named *Ctenitopsis* which includes free-veined species of both *Heterogonium* and *Tectaria*; in my view it is not a natural group. Copeland has included such species in *Ctenitis*.

Psomiocarpa Presl.

Epim. Bot.: 161 (185).

The single species has sterile fronds which are small but bipinnate, with the same frond-form as some Philippine species of *Tectaria* sect. *Sagenia*, but the fertile fronds have extremely small pinnules quite covered with sporangia. M.G. Price has found plants intermediate between this and a bipinnate species of *Tectaria*. Pichi Sermolli (1977: 465) has wrongly placed this genus near *Ctenitis*.

Aenigmopteris Holttum

Blumea 30: 1-11 (1984).

The five species have elongate fronds with many pinnae which are more finely dissected than those of any species of *Tectaria* sect. *Sagenia*; pinna-lobes, which are themselves deeply lobed, are connected by narrow wings along the pinna-midrib and thus resemble *Lastreopsis* but the margin of the wing is not thickened and the rachis is not winged; as in *Tectaria* sect. *Sagenia* there are thick hairs between veins on the upper surface.

Genera having unicellular cylindric glands

The following four genera agree in having unicellular cylindric glands on the stalks of sporangia, in many species also on the margins of indusia and/or appressed to veins; they agree also in having the chromosome number 41, but they differ from each other in many ways.

Ctenitis C. Chr.

Verdoorn, Manual Pterid.: 544 (1938).

This was originally named *Dryopteris* subg. *Ctenitis* in Christensen's *Monograph of the genus Dryopteris* (part 1: 82-112, 1913; part 2: 31-93, 1920). He there dealt only with American species and defined the subgenus very broadly. In my recent study of all palaeotropic species I have felt obliged to limit a genus named *Ctenitis* by excluding Christensen's groups of *Dryopteris subincisa* (*Megalastrum* of the present conspectus) and of *Dryopteris protensa* (*Triplophyllum* Holttum 1986). I have not attempted to assess critically all the other neotropic groups recognized by

Christensen but believe that they would accord to my definition of *Ctenitis*. As thus limited, the genus comprises about 100 species and is considerably diversified in both the Old World and the New. In the Old World there are three distinct groups of species: the group of *C. submarginalis* (Langsd. & Fisch.) Ching (type species of the genus) which is mainly American but extends to Africa and the Mascarene Islands, and the species of mainland Asia, Malesia and the Western Pacific which are divisible into two groups which are sharply distinct from each other in both scales and spores (Holttum 1985). Two Hawaiian species are very different in spores from any in the western Pacific and I think also from any in the Americas. Thus the genus *Ctenitis*, worldwide, needs a new conspectus and I do not propose formal subdivisions for the Malesian species.

Ctenitis differs from *Tectaria* in its glands, its fragile gland-fringed indusia, in having abundant scales which are at least in part clathrate on all the smaller axes of the frond, also in having fronds which in almost all species are more finely divided, the ultimate leaflets almost always deeply lobed and always with free veins.

Lastreopsis Ching, emend. Tindale

Contr. N.S.W. Nat. Herb. 3: 249-339 (1965).

In Tindale's monograph of the genus 33 species are recognized; since then a few more have been added. Their fronds are finely divided somewhat as in *Ctenitis* but differ in scales, which are more like those of *Tectaria*, and in the thickened decurrent basiscopic margins of leaflets which form wings on the axes to which they are attached. The hairs in this genus are notably varied; ctenitoid hairs occur in most species, but in some the hairs on the upper surface of axes of the frond are rigid and more or less acicular, not contorted on drying; such hairs are characteristic of *Megalastrum*, described below. *Lastreopsis* is pantropic in distribution but the monograph by Tindale does not indicate any subdivision into natural groups of species. I suggest that the nature of the hairs on the upper surface of axes of the frond might offer clues to the distinction of sections within the genus. My impression is that the species of West Africa need more study.

Pleocnemia Presl. emend. Holttum

Kew Bull. 29: 341-357 (1974).

This genus of 19 species, mainly Malesian, was based by Presl on the venation (which agrees with *Tectaria* sect. *Sagenia*) and on the exindusiate sori of the sole original species, but there are also indusiate species and Presl did not notice the two most distinctive characters, namely the presence of teeth in the sinuses between pinnule-lobes and of cylindric glands which are usually yellow or orange in contrast to the usually pallid glands of most species of *Ctenitis*. The fronds of mature plants of all species are large, and the pattern of vascular strands in the stipe is more complex than in the other genera.

Coveniella Tindale

Gard. Bull. Sing. 39:169 (1986).

Caudex slender, long-creeping, with closely approximate fronds; scales very short, consisting of short cells which are not clathrate, those on the rachis and costae grading to ctenitoid hairs; short slender pluricellular hairs abundant near bases of stipes, variably abundant on both surfaces of the rachis, unicellular glands sparsely present on various parts of the fronds; fronds simply pinnate, pinnae entire and narrowed near their bases, the lower ones stalked, not articulate to the rachis; veins in pinnate groups, the basal veins in each group free, successive ones anasto-

mosing to produce short free excurrent veinlets; sori exindusiate, short cylindric glands present on sporangium-stalks; n = 41 (S.K. Roy).

Only one species is known, in Queensland and north-eastern New South Wales; it was originally named *Polypodium peocilophlebium* Hook.

Genera lacking glands

The following five genera agree with the gland-bearing ones in having 41 chromosomes but in other ways are not closely related. They show varied indications of relationship to either *Tectaria* or *Ctenitis* except *Cyclopeltis* which is probably related to *Coveniella*. A sixth genus, *Pseudotectaria*, has not yet been examined cytologically.

Ataxipteris Holttum

Blumea 30: 10 (1984).

The sole species of this genus, from southern China and Japan, has fronds agreeing exactly in form and venation with those of some free-veined species of *Tectaria* but has abundant rachis-scales much like those of *Ctenitis*; its spores are similar to those of one palaeotropic group in *Ctenitis*.

Pteridrys C. Chr. & Ching

Bull. Fan Mem. Inst. Biol. Bot. 5: 129 (1934).

Scales narrow as in *Tectaria* but with strongly cordate base; fronds simply pinnate; pinnae deeply lobed with a tooth in each sinus between lobes, the tooth projecting out of the plane of the pinna; veins free, arranged as in free-veined *Tectaria*; ctenitoid hairs few, near the bases of pinnae, sometimes on both surfaces of costae.

This genus of seven species is distributed in mainland S.E. Asia, Ceylon and Malesia. The sinus-teeth are like those of *Pleocnemia* but in other ways the two genera differ considerably.

Triplophyllum Holttum

Kew Bull 41:239 (1986).

As arranged by Holttum there are twenty species with a centre of distribution in Africa; there are five species in tropical America and two in Madagascar. Most species have been placed by recent authors in *Ctenitis*, but two have anastomosing veins and so have been assigned to *Tectaria*, though their vein-branching is mainly anadromous and their pattern of anastomosis is slightly different. Their scales are *Tectaria*-like, also their spores. They all have a long-creeping caudex and fronds of young plants are almost symmetrically tripartite. *T. dicksonioides* (Fée) Holttum in Brazil has minute spherical glands on the lower surface.

Cyclopeltis J. Sm.

Bot. Mag. 72 (Comp.): 36 (1846).

Scales narrow, sometimes with dentate margins, the teeth consisting of outgrowths from single cells; fronds simply pinnate, the pinnae unlobed and articulate to the rachis, sessile with cordate basiscopic bases which overlap the upper surface of the rachis; veins free, their lower branches not nearly reaching the margin; very short hairs consisting of several cells present on both upper and lower surfaces of rachis and costae, more abundant on the lower surface; sori covered with peltate indusia; spores similar to those of some species of *Tectaria*.

A genus of about six species, rather uniform and widely distributed in tropical America, more diversified in SE Asia and Malesia. The teeth on the margins of scales, where present, differ from those of other palaeotropic genera, the teeth of which are formed by the projecting common wall between adjacent marginal cells.

Megalastrum Holttum, *gen. nov.*

"Group of *Dryopteris subincisa*" C. Chr., K. Danske Vid. Selsk. Skr. VIII, 6: 59 (1920).

Caudex crassus, modice arborescens; stipes dense paleaceus, paleis breviter dentatis vel integris; lamina frondis magna, copiose bipinnata, pinnulis profunde lobatis, pinnis infimis basin basiscopicam versus auctis; venae omnes liberae, infimis supra basin sinuum inter lobos pinnularum terminatis; paleae axium frondis non clathratae, dentatae vel integrae, plerumque multae; rhachides pinnarum costaeque pinnularum supra pilosae, pilis acicularibus, pluricellularibus, in sicco non contortis; glandulae cylindricae unicellulares desunt; indusia, ubi adsunt, magna, firma, pilosa; sporae minute spinulosae; n = 41.

Type species: **Megalastrum villosum** (L.) Holttum, *comb. nov.* (*Polypodium villosum* L., Sp. Pl. 1093 (1753).

In his monograph of 1920 Christensen included thirty neotropic species in this group as part of his subgenus *Ctenitis*. John Smith, who had seen some of them in cultivation at Kew, included them in the genus *Lastrea*, calling them "the *villosa* group"; he recognized their distinctive character and suggested (1875: 216) that they might form a genus for which the name *Megalastrum* would be appropriate. In this as in many other ways he showed greater understanding (gained by observation of living plants) than most of his contemporaries, and I am happy to adopt his suggested name. T.G. Walker (1966), in Jamaica, found that plants of the type species of *Megalastrum*, each being the outgrowth of a single cell, as in *Cyclopeltis*. found it to be tetraploid. Spores are illustrated on Plate 3.

One species should be excluded from Christensen's original list; it was first named *Polypodium grande* by Presl. In form, venation and thick texture, its fronds are very similar to those of *Ataxipteris* (of China and Japan) but its scales are very different; their marginal teeth are also differently formed from those of the type species of *Megalastrum*, each being the outgrowth of a single cell, as in *Cyclopeltis*.

In Africa there is only one species of this genus, *M. lanuginosum*. In its indusia and spores it agrees closely with *M. villosum*; its distribution extends to Madagascar and the Mascarene Islands, where there are four more species. These African and Mascarene species do not have the dentate scales which are characteristic of most species in the neotropics. New names for them are proposed as follows.

Megalastrum lanuginosum (Kaulf.) Holttum, *comb. nov.*

Aspidium lanuginosum Kaulf., Enum. Fil. Chamisso: 244 (1824).

Megalastrum magnum (Bak.) Holttum, *comb. nov.*

Nephrodium magnum Bak., J. Bot. 22: 142 (1884).

Megalastrum exaggeratum (Bak.) Holttum, *comb. nov.*

Nephrodium crinitum var *exaggeratum* Bak., Ann. Bot. 5: 319 (1892).

Megalastrum lanatum (Fée) Holttum, *comb. nov.*

Phegopteris lanata Fée, Gen. Fil. 246 (1852).

Megalastrum canacae (Holttum) Holttum, *comb. nov.*

Ctenitis canacae Holttum, Kew Bull. 38: 128 (1983).

Pseudotectaria Tard.

Notul. Syst. (Paris) 15: 87, pl. 6 (1955).

The type species, originally named *Tectaria decaryana* C. Chr., has in its supra-basal pinnae a venation comparable to that in *Meniscium* (Thelypteridaceae) but in the basal part of its basal pinnae the venation is more complex and more like that of *Tectaria* sect. *Sagenia* (see C. Chr. 1932, pl. 19). The shape of the basal pinnae shows some resemblance to *Heterogonium*, but the basal basiscopic lobes are not gradually reduced. The outer veins of costal and costular areoles in the basal pinnae of *P. decaryana* are not parallel to the costae and costules as in *Tectaria* sect. *Sagenia* and *Heterogonium*; they are formed by upcurved veins which in fertile pinnae each bears a sorus, meeting to produce one or more excurrent free veinlets. In the second species of *Pseudotectaria, P. crinigera* (C. Chr.) Tard., the pinnae are distinctly lobed with rather widely spaced costules, and the venation throughout (as shown in C. Chr. 1932, pl. 18) resembles that in the basal pinnae of *P. decaryana*. The smaller scales in both species are abundant, narrow, thin, with all cells elongate and showing a clear lumen, contrasting with the rigid opaque scales of *Tectaria*. I suggest that the first four species of Christensen's *Dryopteris* subg. *Ctenitis* (1932: 57-58 and pl. 13, 14) are related to the species of *Pseudotectaria* and should probably be transferred to it (Mme Tardieu-Blot mentioned this possible relationship in 1955); they certainly do not belong to *Ctenitis* as understood in the present conspectus.

Thus I suggest that *Pseudotectaria* represents a development of anastomosis which has occurred on an evolutionary line distinct from that of *Tectaria*, comparable with the parallel development in *Triplophyllum*.

Discussion

In view of the pantropic distribution of *Tectaria* and *Ctenitis* (the largest genera) and the great range of form among the other genera, this group must have had a long evolutionary history during which connecting links have disappeared. There can be no doubt that *Tectaria* and the smaller genera here associated with it are closely allied, and I suggest that there is good evidence for an origin of *Tectaria* in SE. Asia, as free-veined species occur there from which, within the genus now existing, there is every gradation to species with elaborate anastomosis of veins (in Thailand, the distinction between sect. *Tectaria* and sect. *Sagenia* is not quite sharp).

The genera which have unicellular cylindric glands are not a closely allied group. *Pleocnemia* resembles *Tectaria* sect. *Sagenia* in venation but differs in the presence of sinus-teeth and glands, in the former agreeing with *Pteridrys* (which lacks glands) and in the latter with *Ctenitis*. Another genus which lacks glands, *Ataxipteris*, has the frond-form and venation of free-veined *Tectaria* but abundant scales very like those of *Ctenitis*. *Lastreopsis* is near *Ctenitis* (in which it was included by Copeland) in glands but more like *Tectaria* in scales and has more variable hairs and more varied branching of fronds. The sole species of *Coveniella* has no clear resemblance to any other genus; its simple pinnae and their venation are nearest to those of *Cyclopeltis* and the glands on sporangium-stalks resemble those of *Ctenitis*, but there are now no Australian species of either genus.

The situation is further complicated by the fact that *Tectaria* and closely related genera have the chromosome number 40 (no counts yet for *Psomiocarpa* and *Aenigmopteris*) whereas all the rest have 41. If we assume that 40 is the older number, 41 may have developed on various evolutionary lines. But there are three different genera which appear to show affinities with both *Tectaria* (40) and *Ctenitis* (41): thus no simple evolutionary pattern seems possible.

A C B D

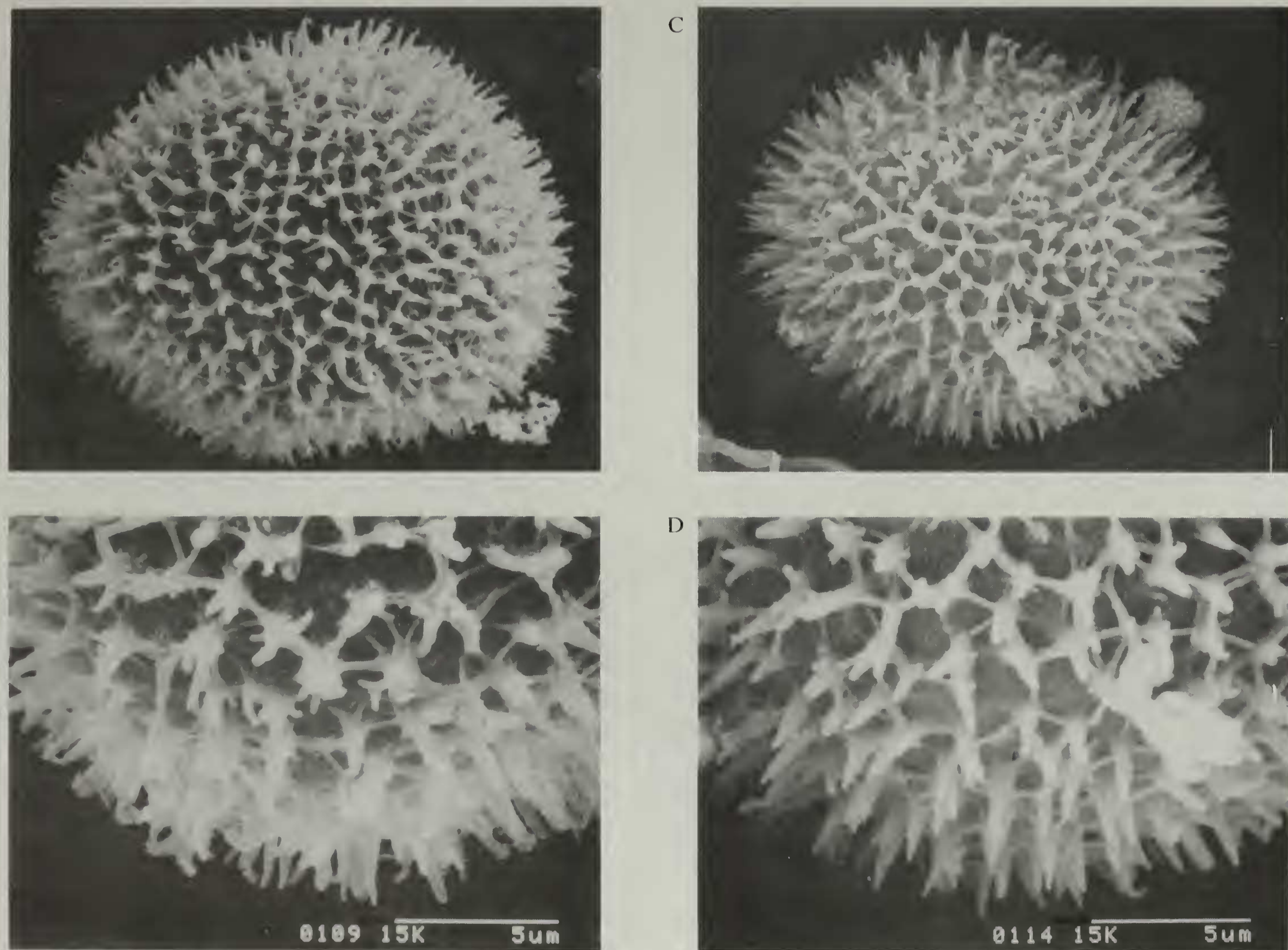
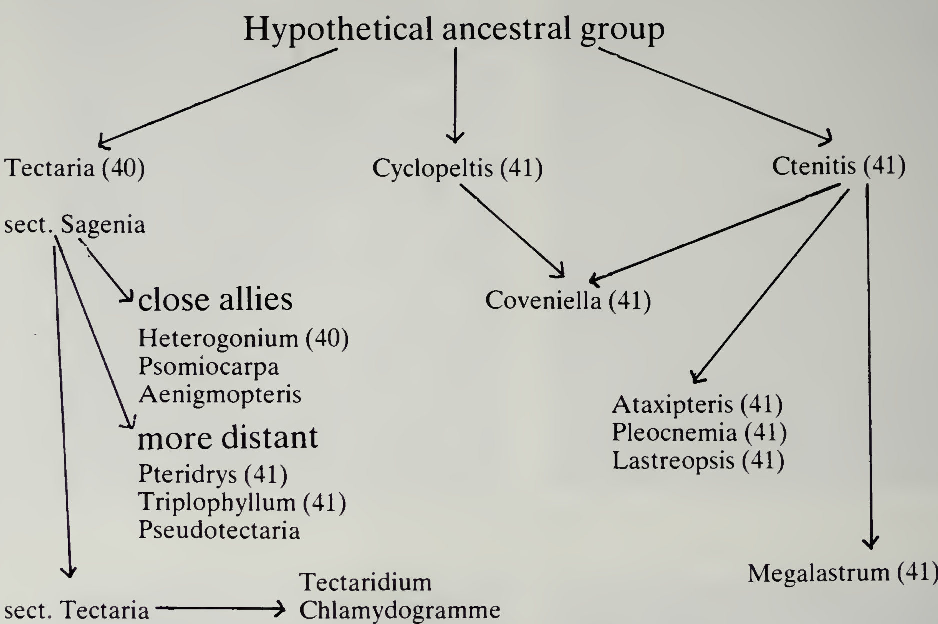


Plate 3. Spores of *Megalastrum*. *M. lanuginosum*: *A* (× 1750), *B* (× 3500); *Gerrard 1933*, Natal (K). *M. villosum*: *C* (× 1750), *D* (× 3500); *Bancroft* s.n. 1850, Jamaica (K).

The puzzle seems to me resolvable by assuming that on rare occasions there has been genetic interchange between species of Tectaria and *Ctenitis*. The existence of the single species of *Ataxipteris* (41) with some characters in common with *Tectaria* and some with *Ctenitis* looks like the result of such a process. *Pleocnemia* (41), with 19 species spread over a wide area, may be the result of a gene interchange which took place at an earlier time.

I suggest that such interchanges may be summarized in the form of a diagram.



Notes on Neotropic Genera

Pichi Sermolli (1977) recognizes the following genera which I regard as allied to *Tectaria: Dictyoxiphium* Hook., *Amphiblestra* Presl, *Pleuroderris* Maxon, *Camptodium* Fée, *Fadyenia* Hook. and *Atalopteris* Maxon & C. Chr. All these except *Atalopteris* are monotypic and clearly related to *Tectaria* and are united to *Tectaria* by Tryon & Tryon (1982: 470). *Atalopteris* is clearly related to *Ctenitis* and is considered separately below.

Dictyoxiphium has simple fronds with the venation of *Tectaria* sect. *Tectaria*. They have continuous indusiate submarginal sori, in which they agree with *Chlamdogramme* but the fertile ones are not contracted. *Dictyoxiphium* hybridizes with *Tectaria incisa* Cav. to produce *Pleuroderris* (Wagner 1978). *Amphiblestra* has deeply lobed fronds with the venation of *Tectaria* sect. *Tectaria* and continuous submarginal exindusiate sori. The recognition of *Dictyoxiphium* and *Amphiblestra* as distinct genera is largely a matter of convenience.

Camptodium has small opaque fronds with free veins arranged as in some palaeotrophic species of *Tectaria* sect. *Sagenia* but is not nearly related to them. It is specialized in adaptation to growth on limestone rocks in sheltered places. *Fadyenia* is also reduced and specialized, with a rather irregular anastomosis of veins not quite like that of sect. *Sagenia*.

The species first named *Polypodium grande* by Presl, referred to above under *Megalastrum*, is very large but with a venation essentially similar to that of *Camptodium*, agreeing also in its opaque fronds but differing in its peculiarly dentate scales. This species needs further study; I suggest that it should have generic rank.

Another species which needs further study is *Tectaria brauniana* (Karst.) C. Chr. This has deeply pinnatifid fronds of thin texture, its lobes again deeply pinnatifid; its veins are free, arranged as in free-veined palaeotropic species of sect. *Sagenia*. It is peculiar in its slender creeping caudex bearing thin translucent scales and in the presence of minute sessile or subsessile spherical glands on the lower surface and on indusia; these glands are similar to those of *Triplophyllum dicksonioides* (Fée) Holttum and I have seen no similar ones on any other species of *Tectaria*.

Atalopteris has sterile fronds similar in form to those of the type species of *Ctenitis* but differing in crenate pinna-lobes and the separation of one or more lobes as pinnules on basal pinnae. Its fertile fronds have greatly contracted pinnae bearing exindusiate sori in which the sporangium-stalks bear glands as in *Ctenitis*. There are also abundant cylindrical glands on the lower surface of sterile pinnae. The small scales on rachis and costae are thin with light brown cell-walls; I see no isodiametric cells and the scales are not so clearly clathrate as those in *Ctenitis submarginalis*.

Artificial Key to the Palaeotropic Genera

1. Teeth present at the bases of sinuses between pinna- or pinnule-lobes, the teeth projecting out of the plane of the lamina (in some species present only in distal sinuses)
   2. Fronds simply pinnate with free veins; no glands on lamina or in sori .... *Pteridrys*
   2'. Fronds mostly bipinnate, their veins forming at least costal areoles; cylindric or ovoid unicellular glands present on stalks of sporangia and/or on lower surface of lamina .... *Pleocnemia*

1'. Teeth of this kind lacking
   3. All axes of the frond bearing copious scales, the smaller ones at least partly clathrate with isodiametric cells
      4. Cylindric glands present on young indusia and elsewhere; pinnae (and usually pinnules) deeply lobed, the basal basiscopic vein in each lobe arising from the costule of the lobe and ending above the base of the sinus .... *Ctenitis*
      4'. Cylindric glands lacking; pinnae less deeply lobed, the basal basiscopic vein in each lobe usually arising from the costa of the pinna and ending below the base of the sinus ... *Ataxipteris*
   3'. Smaller axes of the frond bearing scales which are few (except in *Megalastrum* and *Pseudotectaria*) and not thus clathrate; unicellular glands lacking except in *Lastreopsis*
      5. Veins in sterile fronds anastomosing copiously; free veinlets present in areoles (including those along the costa) variously directed and in most species forked
         6. Fertile fronds greatly contracted and bearing indusia
            7. Sterile fronds simple; fertile ones irregularly deeply lobed; indusia reniform *Tectaridium*
            7'. Sterile fronds pinnate; pinnae of fertile fronds linear, with continuous indusia along each side of the costae .... *Chlamydogramme*
         6'. Fertile fronds not greatly contracted, or if so lacking indusia .... *Tectaria* sect. *Tectaria*
      5'. Veins anastomosing to form costal areoles which lack free veinlets, or all veins free
         8. Some thick multicellular hairs present between veins on the upper surface, at least near sinuses between lobes; where veins anastomose, the costal areoles narrow and of even width
            9. Basal basiscopic lobe or pinnule of basal pinnae longer than the other lobes or pinules
               10. Fronds not greatly longer than wide
                  11. Veins anastomosing in some species; fertile fronds, if greatly contracted, not bearing very small pinnules .... *Tectaria* sect. *Sagenia*
                  11'. veins all free; fertile fronds bipinnate with very small pinnules; no indusia .... *Psomiocarpa*
               10'. Fronds greatly longer than wide, with many pinnae gradually increasing in size downwards .... *Aenigmopteris*
            9. Basal basiscopic lobe of basal pinnae much reduced, these pinnae widest at about mid-length .... *Heterogonium*
         8'. No thick hairs present between veins on upper surface; where veins anastomose (*Triplophyllum* and *Pseudotectaria*) the costal areoles not elongate nor of even width
            12. Pinnae entire or slightly lobed; lateral veins in pinnae forming pinnate groups, basal veinlets in each group, where free, not nearly reaching the margin

13. Veinlets all free; pinnae articulated to rachis .... *Cyclopeltis*
13'. One or more pairs of veinlets joining to form a short excurrent veinlet; pinnae not articulated
    14. Anastomosis confined to suprabasal veinlets .... *Coveniella*
    14'. Anastomosis, where it occurs, including basal veinlets .... *Pseudotectaria*

12'. Pinnae various, in almost all cases at least deeply lobed; most free veins reaching or nearly reaching the margin
    15. Fronds very large, bipinnate, arising from a massive erect caudex; upper surface of axes of frond bearing multiseptate thin-walled acicular hairs .... *Megalastrum*
    15'. Fronds never very large, pinnae various; caudex not massive and erect; hairs on upper surface of axes of frond either firm and terete or ctenitoid
        16. Bases of leaflets decurrent as a narrow wing with thickened margin; fronds of young plants not tripartite; hairs on upper surface of axes various; glands present on lower surface and on sproangia .... *Lastreopsis*
        16'. Bases of leaflets not thus decurrent; fronds of young plants tripartite except in *T. varians*; hairs on upper surface of axes always ctenitoid; no cylindric glands present .... *Triplophyllum*

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Postscript

When writing the above in early 1986 I did not know of the publication by S.K. Roy and A.N. Rao of a paper entitled *A brief cytotaxonomic survey of Singapore ferns* (Journal of the Singapore Academy of Science, 14: 53-64, 1985). One observation published in that paper is relevant to the present discussion of *Tectaria* and allied genera.

On p. 60 is Roy's report that a chromosome count from a plant of *Heterogonium sagenioides* showed n = 41, illustrated in fig. 36, whereas in an Appendix to my book on the ferns of the Malay Peninsula (1955) Manton had reported n = 40 for the same species, with her figure 15. In writing the present paper I assumed Manton's n = 40 to be correct.

In view of this discrepancy, and of the fact that the illustration published by Roy and Rao does not provide clear evidence, I wrote to Prof Manton to ask whether she could add any further information. Her reply is that she has re-examined her preparation from a plant originating in Singapore, in consultation with Dr T.G. Walker (Newcastle upon Tyne), and that they confirm the original report of n = 40. Dr Walker reports also that he made preparations from a plant of *Heterogonium pinnatum* (Copel.) Holttum cultivated at Kew (origin G. Mulu, Sarawak, *A.C. Jermy 13318*) and that this showed n = 80; Manton's report on this species was n = 80-82, with a note that better material was needed.

Much more evidence on the chromosomes of species in this group of genera is desirable.

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